Redescription of a unique feather star (Echinodermata: Crinoidea: Comatulida: Comasteridae) with the diagnosis of a new genus

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Abstract.—A new genus, Aphanocomaster, is erected for Comaster pulcher A. H. Clark, which is known only from the holotype. The genus is similar to Comaster in having an apparent cryptosynarthry in the primibrach series, the first brachial syzygy chiefly between the first and second brachials on arms arising from the tertibrach series, and a central mouth. It differs in lacking a transverse initial comb tooth. The new genus differs from all other comasterid genera in having secundibrach series of four ossicles series in which both the first and second ossicles and the third and fourth are united by synarthrial articulations.

In the course of revising the Indo-Western Pacific genus *Comaster* L. Agassiz, a re-examination of *Comaster pulcher* A. H. Clark revealed that the single known specimen lacks a critical feature of the genus as currently diagnosed and exhibits another, previously unnoticed characteristic unique to the family. The combination requires removal of the species from *Comaster* and establishment of a new generic name for it. In addition, published descriptions are uniformly incomplete (A. H. Clark 1912, 1918, 1931).

Terms, abbreviations, measurements and symbols are as follows: Centrodorsal: central aboral plate. Cirri: aboral, segmented hooks attached to centrodorsal; Roman and Arabic numerals indicate numbers of cirri/ individual and segments (cirrals)/cirrus, respectively (a range of values is usually given); LW of cirral: length to median width ratio when viewed laterally. Ray: one of five branched series of ossicles radiating from center of specimen. Radial: (n.) first ossicle of a ray or (adj.) a structure associated or oriented with a ray. Axil: ossicle at which a ray branches. Brachitaxis: series

of ossicles following radial or axil and including the next axil; I-IVBr: first through fourth brachitaxes (written out primi-, secundi-, terti-, and tetrabrachitaxis, or tetrabrach series); Arabic numeral immediately following indicates number of ossicles in that brachitaxis (e.g., IIBr2). Arm: unbranched series of ossicles following distalmost axil; brachial (br; plural, brr); arm ossicle; subscript number indicates specific ray ossicle (brachitaxis or arm) counting from first ossicle after preceding axil or radial (e.g., IIBr₂, br₇); WL of ray ossicle: median width to midaboral length ratio when viewed aborally. Synarthry (---) (See "Note" below): articulation typically between first two ossicles of a brachitaxis or arm consisting of two ligament bundles separated by an aboral-oral fulcral ridge, sometimes with midaboral swelling. Cryptosynarthry: synarthry modified as a tight junction, visible externally as a fine line; the articular faces either smooth or with round or elongate, often concentric raised areas (Hoggett & Rowe 1986, fig. 2c). Syzygy (+): articulation between two successive ray ossicles consisting of radiating

ridges and grooves and appearing externally as a perforated line (e.g., br₃₊₄); intersyzygial interval: number of articulations between successive syzygies. Pinnules (P): unbranched segmented appendages arising from alternate sides of successive brachials. and from exterior side of brachitaxes of more than two ossicles: on brachitaxes, subscript Roman numerals indicate brachitaxis from which pinnule arises (e.g., P_{II} on IIBr); on arms, subscripts count pinnules from the most proximal: Arabic numbers and letters refer to pinnules along exterior and interior side of an arm, respectively (that is, the sides away from and toward the extrapolated axis of the preceding axil) (e.g., P_4 , P_c); LW of pinnule ossicles (pinnulars): length to median width ratio. Comb: modification of distal pinnulars of proximal (oral) pinnules producing comblike profile. Disk: central visceral mass or, specifically, its oral surface: anal interambulacral area: area on disk surrounded by food grooves and bearing anal papilla. For further discussions and examples of comatulid morphometrics. meristics, abbreviations and symbology, see A. M. Clark & Rowe (1971), Breimer (1978), Hoggett & Rowe (1986) and Messing & Dearborn (1990). In all illustrations, sparse uniform stippling indicates articulations between successive ossicles.

Note: The following descriptions include an exception to standard comatulid symbology. Synarthries are designated by oneem dashes (----), following the usage of Gislén (1934), so that, for example, IIBr4(1-2, 3-4) indicates a secundibrach series of four ossicles in which both the first and second and the third and fourth ossicles are united by synarthry. In comatulid crinoids, the first two ossicles following a radial or axil are joined either by synarthry (sometimes modified as a cryptosynarthry) or syzygy. Typically, only the latter is shown (as a + sign) in written symbology. When a syzygy is not present, a synarthry is assumed in this position (e.g., in IIIBr2, the two ossicles are joined by synarthry). Because the species discussed herein exhibits

an unusual distribution of synarthries, they must be clearly indicated. However, even if additional specimens eventually demonstrate that the distribution of synarthries described below is an abnormality, the unique combination of other features exhibited by this specimen requires diagnosis of a new genus, as follows.

Aphanocomaster, new genus

Diagnosis.---A genus of Comasteridae with IBr2 ossicles apparently united by cryptosynarthry; IIBr2(1-2) and 4(1-2), 3-4; IIIBr2(1-2), 4(1-2, 3-4) and 4(1-2, 3 + 4) [possibly also 2(1 + 2)]; in brachitaxes of four ossicles, the second ossicle (IIBr₂ and IIIBr₂) laterally enlarged exteriorly to accommodate robust base of P_{II} and P_{III}, respectively; first brachial syzygies chiefly $br_{1+2,3+4}$ on arms arising from IIIBr; br₃₊₄ alone on exterior arms arising from IIBr; comb teeth tall, triangular or spadeshaped, confluent with exterior lateral margin of pinnular; initial tooth sometimes slightly twisted, but not oriented transversely; mouth central; anal papilla midway between mouth and disk margin.

Type species.—*Comaster pulcher* A. H. Clark (1912), by monotypy.

Etymology.—From aphanes $(\alpha \phi \alpha \nu \epsilon \zeta)$, unseen, invisible, secret, obscure (Brown 1978), and the genus name *Comaster*. Gender is masculine.

Distribution.—Known only from a single station in the Kei Islands, Indonesia, 0–52 m (A. H. Clark 1931).

Remarks.—A. H. Clark (1921) and Gislén (1934) considered the few records in comatulids of four-ossicle brachitaxes consisting of two synarthrial pairs as abnormal. They recorded this pattern in only three species: *Cyllometra manca* (Carpenter) (Colobometridae) (originally as *C. anomala* A. H. Clark), *Heterometra quinduplicava* (Carpenter) (Himerometridae) and *Adelometra angustiradia* (Carpenter) (Antedonidae). A. H. Clark (in A. H. Clark & A. M. Clark 1967) suggested that the single known specimen of *A. angustiradia* might be a juvenile *Himerometra* or related genus, but placed it in the Antedonidae on the basis of its cirri and pinnules. Messing (1975) noted IIBr4 without IIBr₃₊₄ in several specimens of *Crinometra brevipinna* (Pourtalès) (Charitometridae), but did not otherwise identify the articulation between the third and fourth ossicles.

If, in specimens collected in the future, brachitaxes with two pairs of synarthries prove to be abnormally doubled forms of the much more widespread (among comatulids) brachitaxes of two ossicles united by synarthry, a new genus still must be erected for the type specimen of *Comaster pulcher*. No genus currently exists in the Comasteridae with the combination of features exhibited by this specimen: first brachial syzygy chiefly $br_{1+2,3+4}$, both IIIBr2(1-2), and IIIBr4(1-2, 3 + 4) present: no initial transverse comb tooth; mouth central. Only if the IIIBr4(1-2, 3 + 4) are also highly unusual and all brachitaxes are normally of two ossicles in future specimens would pulcher fall within a currently recognized genus: Comissia (Hoggett & Rowe 1986).

Aphanocomaster pulcher (A. H. Clark, 1912) Fig. 1

Comaster pulcher A. H. Clark, 1912:22.– 1918:37, 40, 275, pl. 14, figs. 14, 15.– 1931:443–444, pl. 50.—Gislén, 1919:14.

Holotype.—University of Amsterdam, Zoological Museum, U.Cri.-2114. Siboga Expedition Station 257, Du-roa Strait, Kei Islands, Indonesia, 0–52 m, 11 Dec 1899. 1 specimen.

Description.—Centrodorsal a thick, rounded pentagonal disk, 4.1 mm across (Fig. 1a). Aboral pole slightly depressed, with cirrus sockets encroaching on margin. Cirri XXXIV, 15–17, up to 11.2 mm long, in crowded double marginal row; first segment short, second with LW = 1.5-2.0; third segment longest, with LW 2.8; fourth and following segments decreasing in length, becoming compressed and slightly expanded distally; eighth segment with LW = 1.1-1.3; one or two segments preceding penultimate with LW = 1.0-1.1 (Fig. 1b, c). Fourth and following segments with low, aboral, subdistal, transverse swelling or ridge, sometimes finely spinulose, narrower on more distal segments, becoming low blunt and triangular on the four to five segments preceding penultimate (Fig. 1d, e). Fourth and following segments shiny. Opposing spine low and wide, sharp or blunt.

Arms 35, all in single plane, none complete. Radials very short, just visible. IBr2 ossicles joined by tight articulation, probably cryptosynarthry (see remarks). IBr₁ very short, WL = 4.5-5.0, completely separated or just touching at proximal corners. and slightly narrower distally so that adjacent IBr, are separated by V-shaped gap (Fig. 1a). One IIBr2(1-2) bearing IIIBr4-(1-2, 3-4) exteriorly and IIIBr4(1-2, 3-4)3+4) interiorly; nine IIBr4(1-2, 3-4) bearing nine IIIBr2(1-2) [one of these with a close articulation; possibly IIIBr2(1 + 2)] and three IIIBr4(1-2, 3 + 4) [two of the latter arising from one IIBr4]. IIIBr developed in pairs or interiorly on IIBr. One interior IVBr2(1 + 2)?; the articulation uniting its ossicles a tight line similar to syzygy on proximal brr, but perforations not clearly visible. First ossicles of adjacent brachitaxes beyond the first (II-IVBr₁) joined interiorly for most or all of their length; adjacent IIBr and following brachitaxes separated interiorly by narrow U-shaped gaps; gaps becoming narrower between more distal brachitaxes, but remaining distinct between adjacent arm bases. Width at IIBr₄ axil 1.6 mm (1.3 at IIIBr axil).

Br₁ slightly longer exteriorly; adjacent br₁ joined interiorly; in arm bases with br₁₋₂ united by synarthry, br₂ cuneate and projecting exteriorly to accommodate base of large P₁. Proximal brachials otherwise oblong as far as br₆₋₈, WL = 1.7; triangular or almost so by about br₉₋₁₀, WL = 1.9. Middle brachials triangular, WL = 1.3–1.4. Distal brachials elon-



Fig. 1. a–i. Aphanocomaster pulcher (A. H. Clark), holotype. a. Aboral view showing centrodorsal, bases of cirri, bases of three rays, and basal few ossicles of proximal pinnules. b. Cirrus with weak aboral ornamentation. c. Cirrus with strong aboral ornamentation. d. Oblique view of fourth (left) and fifth cirrals showing finely spinulose transverse subdistal ridge. e. Oblique view of tenth (left) to thirteenth cirrals showing transverse aboral swelling narrowing to triangular process on more distal segments. f. P_{II} reconstructed from fragments; most of comb lost. g. P_2 . h. Lateral view of proximal part of comb from a detached oral pinnule showing slightly twisted proximal tooth (arrow). i. Same, oblique view. j. *Comaster distinctus* (Carpenter), lateral view of proximal part of comb from a detached oral pinnule showing well-developed transversely-oriented proximal tooth (arrow). Scale bar: a, 2 mm; b, c, f, g, 1 mm; d, e, h–j, 0.5 mm.

gated, shaped like bent hourglasses, WL = 0.5 (LW = 1.9).

Aboral surface of rays smooth, somewhat flattened. On II and IIIBr4(1—2, 3—4), II and IIIBr₂ cuneate with exterior lateral margin projecting for articulation of very robust P_{II} and P_{III} ; P_{II} and P_{III} so large that the ossicle bearing them almost appears as an asymmetric axil (Fig. 1a). Synarthries on brachitaxes sometimes weakly swollen midaborally. Distal margins of mid-arm brachials finely dentate but not flared or thickened. Distal brachials smooth. Epidermis fairly thick, obscuring several articulations.

First brachial syzygies chiefly $br_{1+2,3+4}$ on arms arising from IIIBr; br_{3+4} alone on exterior arms arising directly from IIBr4 (one with $br_{3+4,4+5}$, another with br_{4+5} instead) (Fig. 1a). On one ray, the exterior arms arising from a pair of adjacent IIIBr2 both lack br_{1+2} (one has br_{3+4} , the other is broken at br_2); interiorly, one of these IIIBr2 bears an arm with $br_{1+2,3+4}$; the other bears a IVBr2(1 + 2) which, in turn, bears an interior arm with $br_{1+2,3+4}$ and an exterior arm with br_{3+4} alone. Next syzygy br_{16+17} . Distal intersyzygial interval chiefly 4 (occasionally 3 or 5).

 P_{μ} of 35+ segments, comb lost; estimated length ≈ 14 mm; very robust at base, tapering to slender and flagellate distally; middle segments longer than broad (to LW = 1.5); no spines visible (Fig. 1f). One detached oral comb of 15 teeth possibly belongs to P_{II} or P_{III} . P_1 of 37 segments with 11 teeth, $L \approx 10.0$ mm; similar to P_{II} but slightly less robust; apparently shorter with fewer segments. P2 of 31-33 segments, 12 teeth, L = 8.2 mm; much less robust than P_1 (Fig. 1g). P_c of at least 26 segments with 6 teeth (tip possibly lost), remaining length = 7.6 mm. P_f of at least 22 segments with 7 teeth (tip possibly lost), remaining length = 5.7 mm. Comb teeth tall, triangular or spade-shaped and at least slightly incurved. confluent with exterior lateral margin of pinnular. Initial tooth sometimes slightly twisted (Fig. 1h, i); no initial transverse tooth. [Compare with initial transverse tooth of *Comaster distinctus* (Carpenter), Fig. 1j.] Comb either rising abruptly with tall first tooth, or developing gradually over 1–3 increasingly tall teeth. Distal teeth smaller & shorter but still well developed. Combs coiling planospirally; present to at least P_{6} .

 P_{g} of 18 segments, no teeth, L = 5.4 mm; most segments (except at base and tip) longer than wide, cylindrical and constricted in middle, LW to 2.0; distal segments with cluster of lateral spines; hooks on last 3 segments. P_7 and P_8 first genital pinnules; spherical gonads developed on fourth-sixth segments. Middle pinnules of 17-18 segments, 6.0 mm long; first two segments short, third and fourth squarish; these first four segments stout; following segments narrower so pinnule tapers to slender tip; most segments little longer than broad with bundle of strong spines along lateral margin. Distal pinnules of 17 segments, 7.2 mm long; first two segments short; following segments elongate (except near tip), and of about equal length but becoming more slender distally; LW increasing from about 3.3 proximally to 5.2 distally (not including basal or distalmost segments).

Disk completely naked; oral integument somewhat transparent with tiny sclerites visible in tissue. Mouth central; anal papilla large, about midway between mouth and disk margin; anal interambulacral area only slightly larger than other interambulacral areas.

Color.—White in alcohol.

Distribution.—Kei Islands, Indonesia. Known only from the type specimen.

Remarks.—The identities of the articulations in several brachitaxes are uncertain. The two ossicles of each IBr2 are joined by a tight articulation that may be either a synarthry or cryptosynarthry. No trace of the external perforations exists that would identify these articulations as syzygies and place the specimen in the genus *Comatula*. The articulation has not been dissociated for detailed examination because the specimen is unique. The articulations between the two ossicles of the single IVBr2, and the IIIBr2 that precedes it, are tight, similar to syzygies on the proximal brachials, but with perforations not clearly visible.

The specimen is in somewhat poorer condition than when last photographed (A. H. Clark 1931). However, the current redescription is substantially more detailed and differs in several important respects from those previously published (A. H. Clark 1912, 1918, 1931). I found XXXIV rather than XXVII cirrus sockets with the longest cirrus segment having LW = 2.8rather than 3 to 4. The previous descriptions refer to a single IIBr2(1-2), nine IIBr4(1-2)(3 + 4), and all IIIBr2(1 + 2). This re-examination clearly shows that syzvgies are not present in the IIBr, and that the IIIBr includes 4(1-2, 3-4), 4(1-2, 3 + 4), 2(1-2) and, possibly, 2(1 + 2).

In addition to the diagnostic characteristics of brachitaxes and pinnule combs, several other features also distinguish A. pulcher from the several nominal cirrus-bearing species of Comaster of similar size: C. fruticosus A. H. Clark, C. brevicirrus (Bell), C. schoenovi A. H. Clark, C. sibogae, A. H. Clark, C. distinctus (Carpenter) and C. serratus (A. H. Clark). In these Comaster spp., the longest cirral is usually the fourth, not the third; cirrals bear well developed aboral transverse ridges with a stronger opposing spine; middle brachials are shorter and usually cuneate with everted spinose distal margins; the first syzygy following br_{1+2} (or br_{3+4} , when present) occurs at br₁₀₊₁₁ to br₁₂₊₁₃; the distal intersyzygial interval is usually 3, not 4, and the disks usually bear at least some slender conical nodules.

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